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Preface

English Nature is grateful to the authors for the opportunity to include this report in its Research Report series. By doing so we hope that there is more chance that the records and knowledge of them will be maintained. The work was however done independently of English Nature and any views expressed are not necessarily those of English Nature and its staff.

Acknowledgements

English Nature and its predecessors have maintained Wistman's Wood as a Nature Reserve in agreement with the Duchy of Cornwall. Albert Knott, David Rogers, Ian Tillotson, and other staff of English Nature and its predecessors have undertaken recordings and maintained the archive for the plot.

Keith Kirby, English Nature

Summary

1. Changes in a population of oak seedlings and associated ground cover, canopy gaps and grazing were recorded from 1973 to 1998 by means of a 25 x 25m permanent plot located in Wistman's Wood, a minimum intervention, upland, oak-dominated, grazed woodland growing on ground covered with boulders.

2. During the study the plot changed from an open glade to a near-closed canopy. Use of the wood, especially by cattle, appeared to have been low initially, and then increased to high levels during the 1980s until restrictions were implemented under an Environmentally Sensitive Area agreement in 1995. Use was highest during the winter months when stock sheltered in the wood.

3. The main changes in the ground vegetation were; 1) mosses, which grew mainly on boulders, fluctuated in abundance partly because livestock knocked moss mats off boulders; 2) grasses, which remained dominant on the ground between boulders, changed in abundance, as common bent *Agrostis capillaris* (initially dominant) and wavy hair-grass *Deschampsia flexuosa* (initially co-dominant) declined and creeping soft-grass *Holcus mollis* invaded apparently because cattle poaching increased, but thereafter the original dominants reasserted themselves; and 4) bracken cover declined substantially mainly due to increased shading.

4. Virtually all recorded saplings were oaks *Quercus robur*. Initially they were abundant and several exceeded 50cm height. Thereafter there was a steady decline in the population as mortality rates increased, sapling height decreased, and the average age of saplings and the number of established saplings both decreased. The number of saplings with at least 5 years growth remained moderate until 1986, but declined steeply to 1995. No sapling grew above the reach of grazing animals, and the prospect for successful recruitment diminished steadily. Germination continued unabated and there were substantial inputs of new oak saplings on average every 4 years. Few germinants lived more than one year, and, more recently, very few more than two. The sapling age-structure became increasingly simplified, but two individuals of 20 years age or more survived to 1998, by which time there had been a limited improvement in numbers.

5. The decline in the sapling population was ascribed to the combined effects of increased grazing and shading. The prospect for future recruitment, and the implications for research and monitoring are discussed.

Contents

Introduction

Woodlands need to regenerate to survive. However, tree regeneration can be unpredictable and take many years to arise. It relies on a combination of factors, some of which are very variable, and many interact with each other. For example, in masting trees, such as oak *Quercus* spp. and beech *Fagus sylvatica*, large crops of seed are produced at irregular intervals. If the mast year does not coincide with the production of a gap, the ground vegetation may become so vigorous that germinating saplings are out-competed. Even where young saplings become established, they can be selectively ring-barked when the local vole population peaks. Thus on different occasions, different species may be favoured or the expected regeneration may not develop at all.

Monitoring regeneration is necessary to make sure that a woodland remains in a 'favourable status', and that the expected response to a management activity is achieved. A recently produced guide on monitoring tree regeneration provides some guidance on issues and applicable techniques (Ecoscope Applied Ecologists 1999), but it is difficult to decide what factors are of key importance and how best to devise a suitable monitoring programme. Should all saplings be recorded or only those above a minimum threshold? Should seed traps be set up? Should the ground flora be recorded? How often is recording necessary? How big should the plots be and need they be permanent? How long will monitoring be required for? What is best monitored with the limited finances available?

Scientific studies should provide an answer to these questions, but long-term studies of tree regeneration are scarce, and demographic information for most woodland species in Britain is scanty (Grime *et al* 1988). Indeed, detailed long-term observations in British woodlands are still quite rare, although their number is increasing (Peterken & Backmeroff 1988; Hall *et al* 1999; Kirby & Morecroft 2000).

This Research Report describes a 25-year study of tree saplings in a permanent plot in Wistman's Wood, a near-natural upland oakwood. The study complements another permanent plot study at the wood, which has records of stand change dating from 1921 (Mountford 1999).

Site details

Location and status

Wistman's Wood (national grid reference SX 612 774) covers 3.5ha and is situated on the Dartmoor plateau, south-west England. It is famous as an outstanding example of high altitude Atlantic oakwood growing at extreme limits (Tansley 1939), and has been legally protected since 1961. The wood is now effectively treated as a 'Research Natural Area', and although no silvicultural management occurs, cattle and sheep have access to all but a small experimental enclosure.

The wood occurs in three main blocks (North, Middle and South Groves or Woods) in the valley of the West Dart river at about 400m altitude. These grow on heavily clittered, south-west facing slopes between a narrow stream floodplain and a grass-moor plateau. The clitter formed from underlying blocks of tabular granite that weathered and slumped during peri-glacial conditions (Brunsden 1964). Within the wood soil is limited: on a few boulders a layer of acid humus has accumulated, and between the boulders there are pockets of free-draining soil with certain brown earth properties. The peat and gley soils above and below the wood appear unable to support tree growth (Greenslade 1968). The climate is both cool and wet (Simmons 1965), although the wood is locally sheltered on the clittered slopes (Greenslade 1968).

Vegetation

The wood conforms to W17 *Quercus petraea-Betula pubescens-Dicranum majus* woodland of the National Vegetation Classification (Rodwell 1991) and stand type 6Bb upland birch-pedunculate oakwood of Peterken (1981).

Penndunculate oak *Quercus robur* is dominant, and occurs as an older generation of stunted and contorted trees, and a younger generation of mainly straight-trunked trees (Proctor *et al.* 1980; Mountford 1999). Rowan *Sorbus aucuparia* is occasional and includes several large epiphytic trees that grow from the tops of the old oaks. A few holly *Ilex aquifolium*, hawthorn *Crataegus monogyna*, hazel *Corylus avellana*, and willow *Salix aurita, S. cinerea* have been recorded (Archibald 1966). The branches of trees are typically covered in a variety lichens and mosses, including several hanging *Usnea* species which are characteristic of the wood. Where litter has accumulated on lateral boughs and in tree tops, masses of moss and grazing-sensitive species occur, such as bilberry *Vaccinium myrtillus*, ivy *Hedera helix* and polypody fern *Polypodium vulgare*.

Ground vegetation varies in response to the presence of boulders, soil and variation in the tree canopy (Roberts & Marren 1971; pers. observations). Boulders are often covered in crustose lichens (mainly *Cladonia* spp.), mossy patches (e.g. *Hypnum cuppressiforme, Plagiothecium undulatum, Polytrichum formosum, Rhytidiadelphus loreus, Scapania gracilis, Dicranum scoparium*), and stonecrop *Sedum anglicum*. Along paths, trampling has destroyed or much reduced this cover. Where soil has accumulated, patches of acid grassland occur, with wavy-hair grass *Deschampsia flexuosa*, common bent *Agrostis tenuis*, sheep's fescue *Festuca ovina*, creeping soft-grass *Holcus mollis*, heath bedstraw *Galium saxatile*, tormentil *Potentilla erecta* and sorrel *Rumex acetosa* frequent. In some deeper shade areas, herbs such as wood sorrel *Oxalis acetosella* and bilberry *Vaccinium myrtillus* occur. Where the canopy has opened the ground vegetation can be well developed, especially where it is protected from gazing by boulders, and wood rush *Luzula sylvatica*, bramble *Rubus fruticosus* agg., bracken *Pteridium aquilinum*, soft rush *Juncus effusus*, ferns and foxglove *Digitalis purpurea* are most prominent. In an experimental enclosure, dense growth of bramble and wood rush has developed (Roberts & Marren 1971).

History

Wistman's Wood lies within the post-glacial zone naturally dominated by oak (Simmons 1964; Bennett 1989). Dartmoor was largely cleared of trees during the Bronze and Iron ages, but Wistman's may be a surviving fragment: certainly the wood is mentioned in documents dating from *c*1620 (Proctor *et al* 1980) and the surrounding bracken fringe suggests a former woodland soil (Simmons 1965). Even until the beginning of this century the wood remained as a fragmented and stunted oak copse (Christy and Worth 1922), but has since undergone substantial change (Proctor *et al* 1980; Mountford 1999). From *c*1900 onwards, the old generation of tress has developed upwards and a wave of marginal oak regeneration doubled the area of the wood. These changes coincide with an amelioration in the climate, but a lull in grazing probably facilitated the wave of oak regeneration.

As part of the Dartmoor commonlands, the wood has been subject to grazing for many centuries (Archibald 1966). Although the area around Wistman's was enclosed in 1818, by 1960 the intake walls had fallen into disrepair and high numbers of cattle and sheep could enter the wood. The effects were revealed in a 0.3ha experimental enclosure erected in June 1965: within a decade regeneration of oak and ground vegetation growth had been substantial (Roberts and Marren 1971). Outside this fenced area, oak regeneration had largely been inhibited and the ground flora remains sparse and dominated by grass (Proctor *et al* 1980). Grazing pressure remained high until the early 1990s, when the tenant reached retirement and grazing intensity was reduced. In autumn 1995 grazing intensity was formally reduced under an Environmentally Sensitive Area (ESA) agreement: the intake wall was resurrected and livestock numbers lowered to a maximum of 75 livestock units in summer and 37 sheep-only livestock units in winter.

Methods

Recording

Concern about the effects of livestock, particularly cattle, lead to the establishment of a permanent plot to 'study the effect of grazing on oak saplings'. This was located in an unenclosed area of the wood, and was first recorded in 1973 by Ian Tillotson working for the Nature Conservancy Council. He selected an area within the wood that formed 'an open glade, surrounded by trees, much favoured by cattle in both winter and summer, resulting in considerable yarding and dunging'. The plot measured 25 x 25m and was located at the north-east end of Middle Wood on roughly level ground.

Records have consequently been made in all years from 1973 to 1998 except 1974 (Table 1). Saplings and ground cover were recorded in the winter (October-December) of 1973 and 1975 to 1998, and in the spring (April-May) of 1978 to 1983 and 1985 to 1998 (Table 1). Sapling location was recorded by taking a bearing and distance from a permanent central post. From 1977 saplings were individually tagged and the vertical height to the topmost live part was taken to the nearest cm.

Table 1: Summary of records made in the unenclosed sapling plot between 1973 and 1998.

Item recorded	Years when winter record made	Years when spring record made
Location of saplings	1973, 1975-98	1978-83, 1985-98
Tagging of saplings	1977-98	1978-83, 1985-98
Height of saplings	1977-98	1978-83, 1985-98
Ground cover	1977-97	1978-83, 1985-98
Extent of bracken cover	1973, 1975	-
Location of large trees	1973, 1976	-
Number and g.b.h. of large trees	1998	-
Location of canopy gaps	1998	-

Ground cover was recorded in four 2x2m permanent plots located approximately 4m to the north, east, south and west of the central post. In the 1996 winter recording only 3 plots were recorded:

the post of the southerly plot had been uprooted and the original location was not identified until the next recording. Cover was recorded using a DOMIN scale; + = <1% cover with 1 individual; 1 = <1% cover with 2-3 individuals; 2 = <1% cover; 3 = 1-3% cover; 4 = 4-10% cover; 5 = 11-25% cover; 6 = 26-33% cover; 7 = 34-50% cover; 8 = 51-75% cover; 9 = 76-90% cover; and 10 = 91-100% cover. Ground vegetation, dung, and bare soil and rock were all recorded, and leaf litter was fully recorded from 1980. All lichen and moss species were grouped together, but vascular plants were identified to species.

Supplementary records were made on some occasions. The extent of bracken cover was sketched on to a chart of the plot in 1973 and 1975. Large trees were plotted on the chart in 1973, and a few that had been overlooked were added in 1976. At the last recording in 1998 the number of large trees was counted and the gbh range measured. At the same time gaps in the canopy were sketched and their age estimated. On several occasions notes were made about grazing pressure. The data has been maintained as an archive by the Nature Conservancy Council at the Yarner Wood Office.

Analysis

Sapling and ground cover data were entered on to a Microsoft Excel Version 7.0a spreadsheet to facilitate sorting, statistical analyses, and long-term storage.

The record of saplings required some interpretation. After 1977, saplings were individually tagged and relocation was mostly unambiguous. Beforehand, individuals had to be cross-referenced using bearing and distance locations. Some saplings proved difficult to find and re-appeared at future recordings: these appear to have been obscured by rank ground vegetation because they were small, perhaps grazed off, and often leafless at the recording date. A few recruiting saplings were overlooked: the probable age of these was determined in the field.

The median of the four DOMIN ground cover scores was calculated, with the + scored as 0.5. For the flora, only the most abundant species were considered. Livestock levels for the intake were not directly recorded. However, the dung and bare soil (i.e. poached ground) scores from the ground cover plots provided a guide to livestock use. Both occurred in low abundance, so the frequency occurrence out of the four plots was used.

Results

Change in canopy cover

Canopy gaps were not plotted in 1973, but the area was described as an open glade surrounded by trees. In 1973, 33 large trees were recorded and a further three, recorded in 1976, appeared to have been overlooked.

The canopy appeared to have closed considerably by the end of 1998. Mortality of canopy trees had been very low and 35 trees remained. Several were multi-stemmed individuals, and stem sizes ranged from 40-140cm gbh, (girth at breast height) mostly falling between 70-90cm gbh. Five canopy gaps were recorded covering <20% of the plot. Two were very small marginal gaps caused by recent crown deterioration, and the three others had apparently persisted from 1973. One of the latter was quite substantial, but most of it was outside the plot with only the margin running along the eastern side of the plot.

Change in ground cover

Virtually a complete record of dominant ground cover, including dung and bare soil, was made each October-November and April-May from 1977 to 1998 (Table 2).

Dung was mostly from cattle and bare soil arose due to cattle poaching, so the frequency occurrence of both measures provided an index of cattle use. Initially numbers appear to have been low, but they increased during the 1980s and remained high until autumn of 1995, when numbers fell with the grazing restrictions of the ESA agreement. Highest combined occurrences were mostly recorded in the spring, because cattle frequently stand in the wood during poor winter weather.

Changes in ground cover were assessed in two discrete groups; (i) lichens and mosses growing on boulders; and (ii) grasses and bracken growing on soil between boulders. Moss cover was substantial but fluctuated slightly, in part because livestock occasionally knocked mats of moss off boulders. Thus, the slight decline in abundance during the 1980s and early 1990s, and increase thereafter, is partly due to the reduction in livestock levels. Lichens were restricted to non-mossy areas on boulders, and their cover declined slightly during the early 1990s, whilst bare rock showed a slight increase during this period.

On the ground between the boulders, grasses dominated the ground cover. Three species were abundant. Initially common bent *Agrostis capillaris* was dominant, with wavy hair-grass *Deschampsia flexuosa* co-dominant. Common bent declined through to 1988, but then gradually recovered to its former levels. In contrast, wavy hair-grass increased slightly during the late 1980s, and then declined back to its original abundance. Creeping soft-grass *Holcus mollis* invaded the plots from 1981. By October 1988 it had invaded all four plots and was at its highest levels between 1986 and 1990, declining thereafter. The records for bracken *Pteridium aquilunum* fluctuate greatly because only the emerging fronds were present in the spring surveys. The autumn records show that bracken cover declined substantially.

Table 2: Ground cover and occurrence of dug and bare soil between 1977 and 1998 in four 2x2m permanent plots located within the sapling plot. Cover was assessed using a DOMIN scale (see section 2 for details). Nr = not recorded.

Date	Median values							Occurrence out of 4 plots	
	Bare rock	Lichens	Mosses	Wavy hair-grass	Common bent	Creeping soft-grass	Bracken	Dung	Bare soil
25.11.77	2.5	3.5	7	3	6.5	0	7.5	0	0
2.5.78	2	3.5	6.5	2	6	0	1.25	1	0
8.11.78	3	3	5	3	7	0	6	0	0
25.4.79	2.5	3	6	3	4.5	0	0.25	1	1
29.10.79	3	3.5	5	2.5	6	0	6	1	0
28.4.80	3.5	3.5	6.5	2.5	5.5	0	1	1	1
30.10.80	3	4	5	2.5	6	0	4.5	0	0
30.4.81	3	3.5	6.5	3	5	0	0.75	3	2
22.10.81	3	3.5	6	3	5.5	2	5	1	1
23.4.82	3	3.5	6.5	2	5.5	Nr	0.5	1	1
27.10.82	3	3.5	5	2.5	4.5	2	3.5	2	1
28.4.83	2.5	3.5	5.5	2	3.5	Nr	0.25	3	1
25.10.83	3	3.5	5.5	3	5	2.5	4.5	2	0
15.10.84	2.5	4	5.5	3	4.5	2	5	1	0
24.4.85	3	3.5	6.5	2.5	3	2	0	2	2
21.10.85	3	3	5	2.5	3.5	2.5	5	1	0
22.5.86	3	3	4.5	3.5	3.5	2.5	0.5	0	2
16.10.86	3.5	3.5	5.5	4.5	5	2.5	5	0	0
21.4.86	3.5	3.5	4.5	3.5	3	4	0	1	4
26.10.87	2	3	6	3	2.5	3.5	3	2	0
4.5.88	3	3.5	6.5	3.5	2.5	4	0	2	4
17.10.88	2.5	3	6.5	3	2.5	4.5	3.5	0	1
26.4.89	3	3.5	6	3	3	5	0	1	2
10.10.89	3	3	6	3.5	4	3.5	2.5	0	4
23.4.90	3	3	5	3.5	3.5	4	1	2	3
18.10.90	3.5	3	6	4	5	3	4	0	2
10.5.91	4	2.5	5.5	4	4.5	2.5	2	2	2
22.10.91	4	3	6	3	4.5	2	3	1	2
11.5.92	4	3	5.5	3	4.5	2	0.75	1	3
9.10.92	4	3	6	3	5	2	3	0	0
11.3.93	3.5	3	6.5	3	4	2	3	3	1
25.10.93	3	2.5	7	3	5.5	1.5	3	1	1
26.4.94	3	2.5	7	2.5	5	1.5	0.75	4	2
12.10.94	3	2.5	6.5	3	5	1.5	3	1	1
11.4.95	3	2.5	7	2.5	5	2	0.5	2	2
23.10.95	3	2.5	7.5	3	6	2	2.5	2	1
30.4.96	3	3	7.5	3	6	2	0.25	2	0
18.10.96	3	2	8	3	7	2	3	0	0
2.5.97	3	3.5	7.5	3	6	4	2	0	0
21.10.97	3	3.5	7	3.5	7.5	2	3	0	0
14.5.98	2.5	3.5	7	2.5	7	2.5	1	2	0

Change in sapling numbers

Table 3: End-of-year change, survival, and recruitment of saplings from 1975 to 1998.

Year	No. alive at start	No. losses	No. of surviving recruits	No. alive at end	% of start population that survived	% of end population tht were recruits
1975-76	45	9	8	44	80	18
1976-77	44	7	21	58	84	36
1977-78	58	10	5	53	83	9
1978-79	53	7	2	48	87	4
1979-80	48	7	1	42	85	2
1980-81	42	5	1	38	88	3
1981-82	38	1	0	37	97	0
1982-83	37	2	31	66	95	47
1983-84	66	25	7	48	62	15
1984-85	48	12	18	54	75	33
1985-86	54	19	12	47	65	26
1986-87	47	19	3	31	60	10
1987-88	31	5	1	27	84	4
1988-89	27	6	0	21	78	0
1989-90	21	6	14	29	71	48
1990-91	29	15	1	15	48	7
1991-92	15	4	1	12	73	8
1992-93	12	5	0	7	58	0
1993-94	7	3	1	5	57	20
1994-95	5	2	0	3	60	0
1995-96	3	0	29	32	100	91
1996-97	32	8	9	33	75	27
1997-98	33	20	9	22	39	41

Virtually all recorded saplings were oaks. At the end of 1997 the first two holly saplings were recorded, and at the end of 1998 two more hollies and a rowan were found.

End-of-year change in numbers was constructed from the start of continuous recording (Table 3). Forty-five saplings were present in autumn 1975, of which 26 were survivors from autumn 1973. In the subsequent 23 years, the number of recruits surviving to their first autumn was three or less in 12 years. Recruitment was substantial in 1977, 1983, 1985, 1986, 1990, 1996, i.e. 6 mast years or approximately one mast year in four. Mortality of second year saplings was very high, particularly from about 1980 to 1995. Mortality rates of earlier cohorts were lower, even during the period 1985-1990. Recent cohorts also declined rapidly, but long-term survival cannot yet be measured. Mortality generally exceeded recruitment, despite short-term increases following mast years.

The net result was a steady decline until 1996 in the number of saplings as observed in autumn, followed by a small recovery. The number of saplings with at least 5 years growth (i.e. those with well-established root systems) remained at about 30 until 1986, but declined steeply to 2 in 1995. By 1998, the population comprised two old individuals, survivors from 1973 (or earlier) and 1978 respectively, supplemented by 20 individuals from recent cohorts.

Table 4: Age structure of the sapling population at each recording date from 1973 to 1998 (continued over page). Values show the number of saplings according to their years of origin

	Year of origin (19..)																								
Date	**<74**	**74-5**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**
25/11/73	26																								
08/10/75	26	19																							
01/12/76	21	15	8																						
25/11/77	19	15	3	21																					
02/05/78	19	15	3	21	2																				
07/11/78	19	15	3	11	5																				
25/04/79	19	15	3	11	5																				
29/10/79	16	15	3	9	3	2																			
28/04/80	14	14	3	8	3	2																			
30/10/80	13	14	3	7	2	2	1																		
30/04/81	13	12	3	7	1	2																			
22/10/81	12	12	3	7	1	2		1																	
23/04/82	12	12	3	7	1	2		1																	
27/10/82	11	12	3	7	1	2		1																	
28/04/83	11	12	3	7	1	1		1																	
25/10/83	10	12	3	7	1	1		1		31															
15/10/84	10	11	3	7	1	1		1		7	7														
24/04/85	10	11	3	7	1	1		1		5															
15/10/85	9	11	3	6	1	1		1		4		18													
22/05/86	8	11	3	6	1	1		1		4		9													
10/10/86	8	11	3	4	1	1		1		2		4	12												
21/04/87	7	11	3	4	1			1				2	6												
26/10/87	6	11	3	3	1			1				1	2	3											
04/05/88	6	10	2	3	1			1				1	1	3											
17/10/88	6	9	2	3	1			1				1		3	1										
26/04/89	6	8	2	3	1							1		2											
10/10/89	6	8	2	3	1									1											
23/04/90	6	8	2	3	1									1											

	Year of origin (19..)																								
Date	<74	74-5	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98
18/10/90	5	6	2		1								1			14									
10/05/91	4	6	2		1									1			5								
22/10/91	4	4	2		1									1			2	1							
11/05/92	4	4	2		1									1			2	1							
09/10/92	4	2	2		1									1				1	1						
11/03/93	3	2	2		1									1				1							
25/10/93	2	2	1		1									1											
26/04/94	2	1			1									1											
12/10/94	1	1			1									1							1				
11/04/95	1	1			1									1							1				
23/10/95	1				1																1				
30/04/96	1				1																1				
18/10/96	1				1																1		29		
02/05/97	1				1																1		25	2	
21/10/97	1				1																1		21	9	
14/05/98	1				1																1		8	5	
07/10/98	1				1																1		6	4	9

The age-structure of the sapling population was identified at all recordings (Table 4). Between 1973 and 1998 the structure became increasingly simplified. Cohorts pre-dating 1973 and from 1974/5, 1976, 1977 and 1978, formed very long-lived populations. Two saplings from these cohorts managed to survive through to October 1998. One exceeded 25 years in age, was grazed-off with two weak basal sprouts to 26cm height growing from a short *c*5cm diameter stump, and had never exceeded 40cm height. The other was 20 years old, was grazed–off with a 15cm long shoot with large leaves growing from a short *c*5mm stout stump, and had never exceeded 27cm height. Recruitment from later cohorts was more episodic and shorter-lived. The population increasingly relied on mast years to top up the slowly declining numbers of old saplings. Accordingly, the initial mixed-aged demography became increasingly polarised, and by the mid-1990s the population had diminished to just a few young saplings and a few persistent old-aged saplings. The limited improvement in the sapling age-structure by the end of 1998 correlated with the reduction in grazing pressure during the 1990s.

Of the recorded recruits, 85% were dead by the autumn of the second year (Figure 1 at end of report). Although mortality was about equally spread between winter (76 deaths) and summer periods (84 deaths), there were four episodes of high mortality; (i) from the start of winter 1983 to end of summer 1984, 25 saplings died; (ii) from start of summer 1985 to end of summer 1987, 39 saplings died; (iii) from start of summer 1990 to end of summer 1991, 21 saplings died; and (iv) over the winter 1997/98, 17 saplings died. Summer mortality was correlated with the sapling number and total sapling height at the start of the period, i.e. losses were greater where initial density and biomass were high, but winter mortality showed no such relationship (Table 5).

Table 5: Correlation matrix showing relationship between number of saplings that died, total and average height change, and sapling number, average height, and total height at start of each period, for twenty summer and twenty winter periods between 1977 and 1998. Values are *r* correlation coefficients and those that are significant ($p<0.05$) and meaningful are in bold.

Summer periods	No. saplings died	Average height change	Total height change	No. saplings start	Average height start	Total height start
Average height change	-0.092	1	-	-	-	-
Total height change	0.067	0.816	1	-	-	-
No. saplings start	**0.465**	-0.202	0.218	1	-	-
Average height start	0.223	-0.172	0.042	0.44	1	-
Total height start	**0.456**	-0.19	0.209	0.962	0.628	1

Winter periods	No. saplings died	Average height change	Total height change	No. saplings at start	Average height start	Total height start
Average height change	0.075	1	-	-	-	-
Total height change	0.021	0.68	1	-	-	-
No. saplings at start	0.019	**0.005**	**-0.615**	1	-	-
Average height start	-0.379	-0.297	**-0.599**	0.662	1	-
Total height start	-0.122	-0.111	**-0.694**	0.959	0.82	1

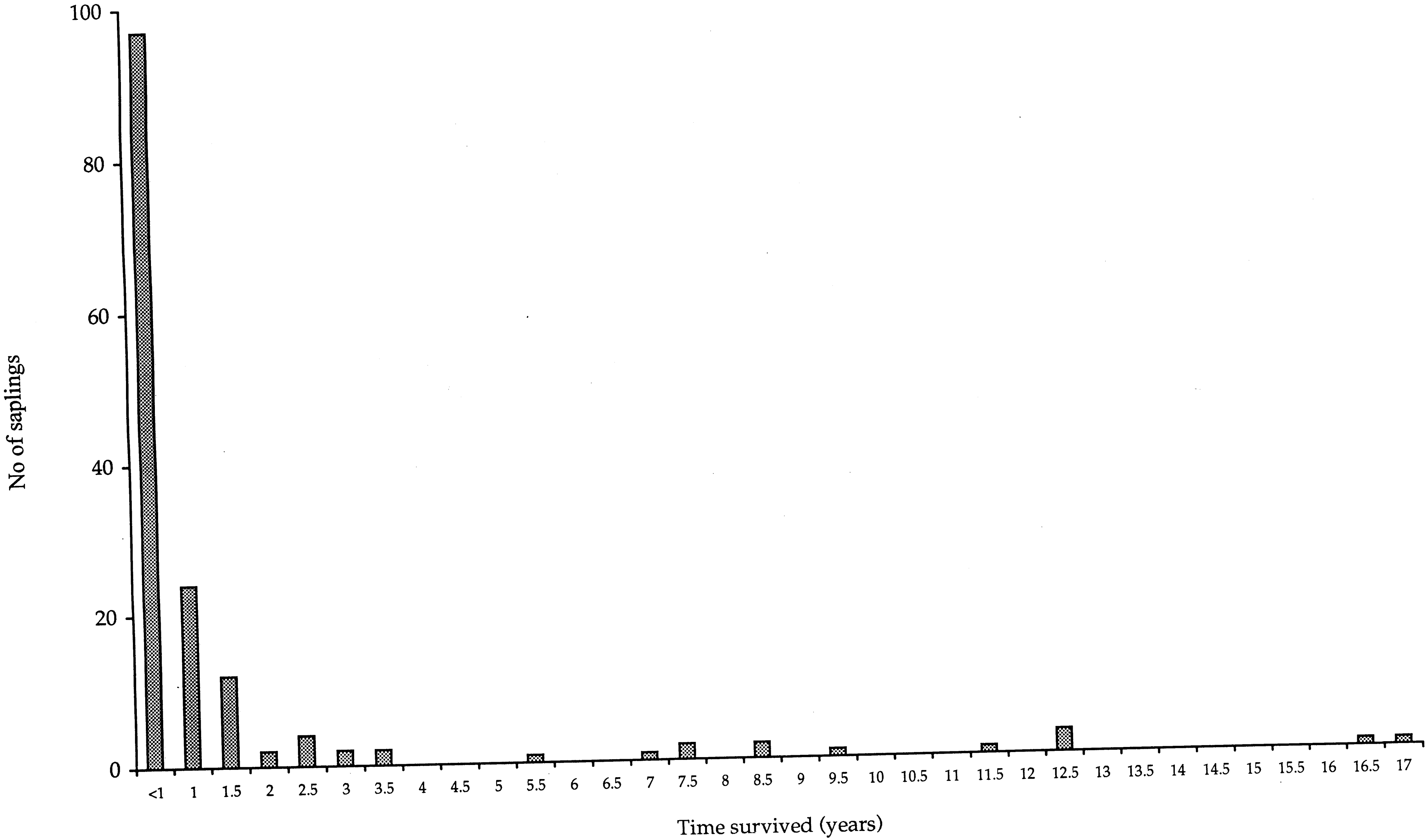

Figure 1. Time that saplings survived after first being recorded.

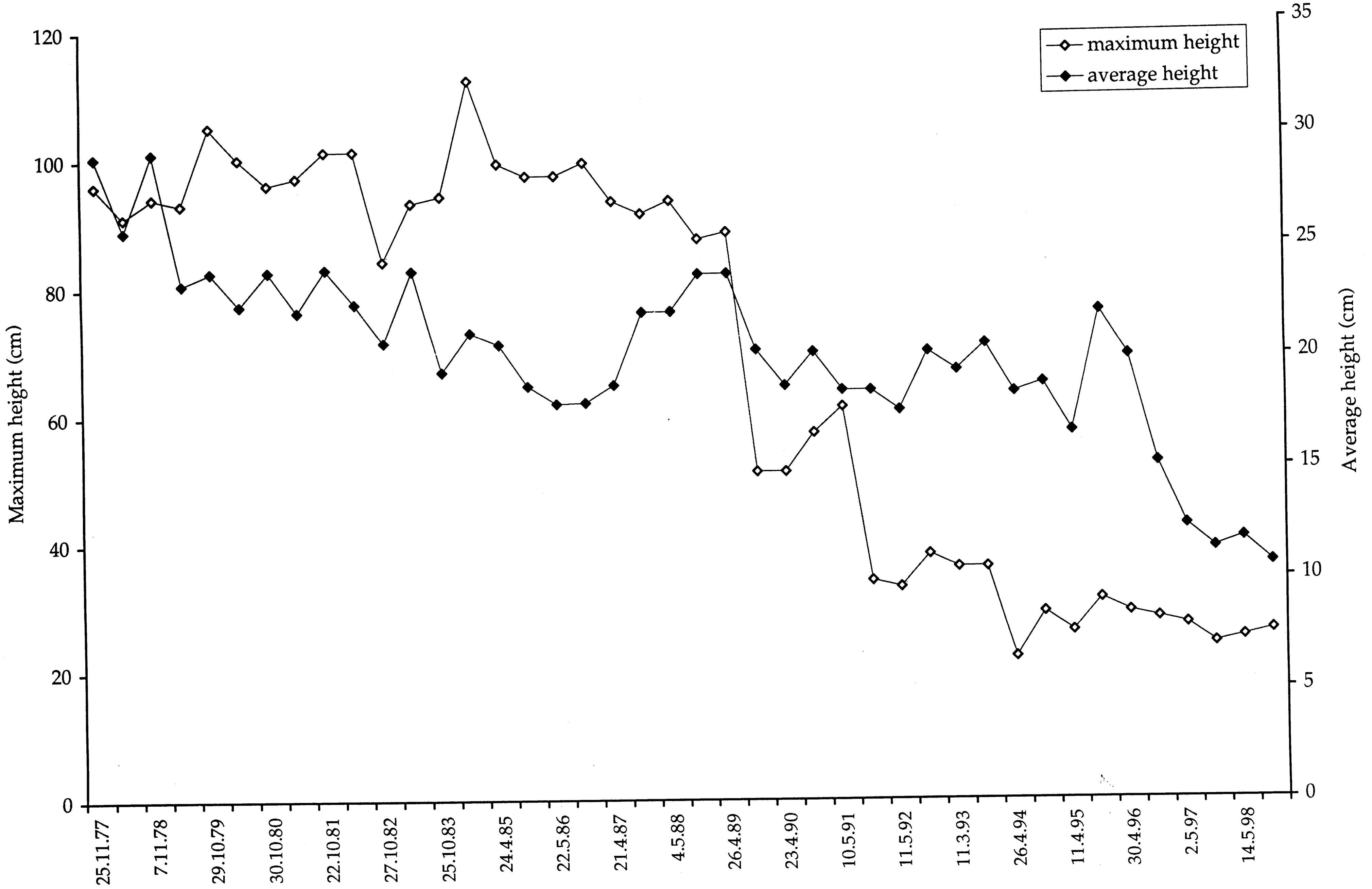

Figure 2. Maximum and average height of saplings between 1977 and 1998.

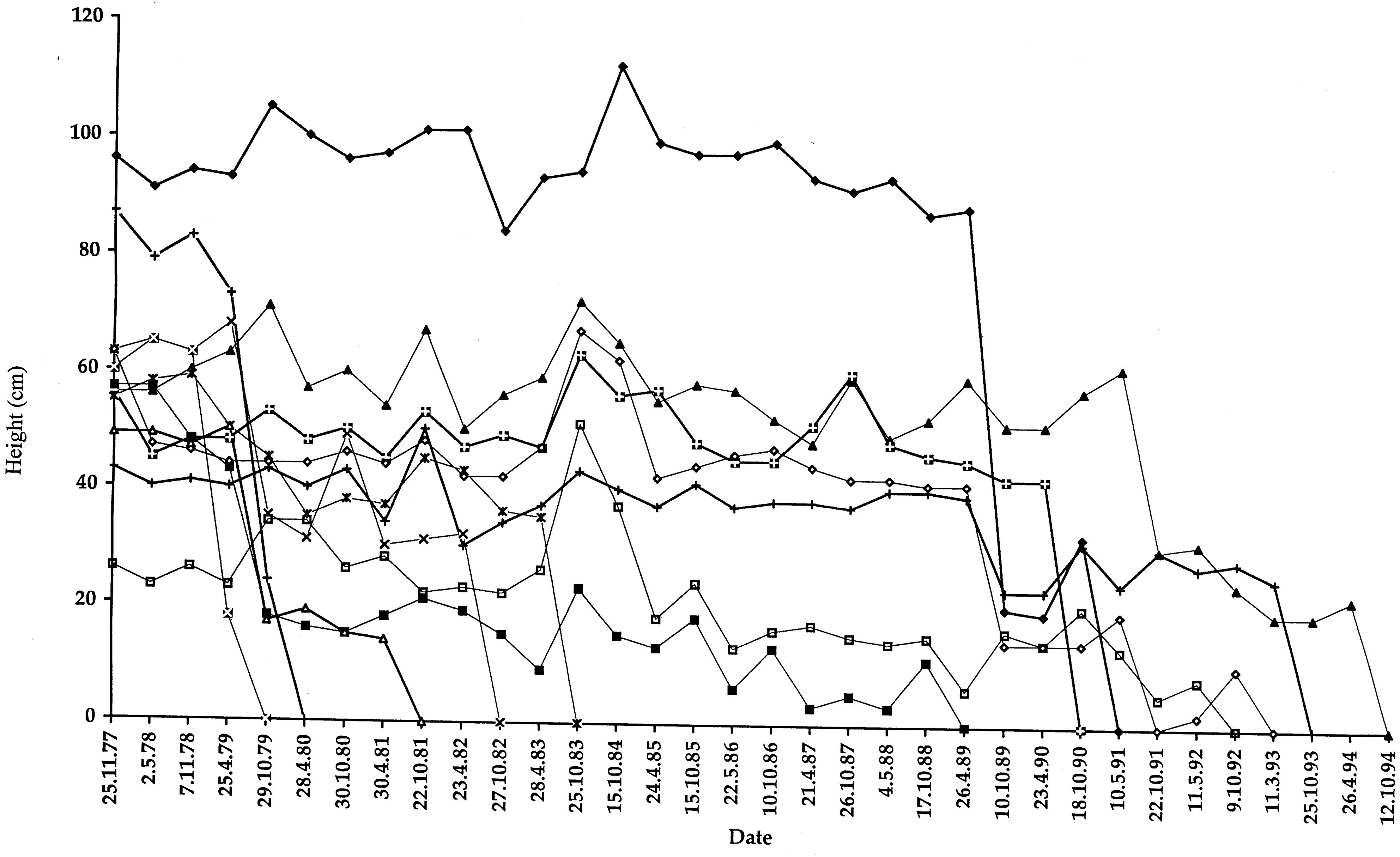

Figure 3. Height change for the twelve tallest saplings that attained 50cm height. The last recorded point for each marked the time of death.

Change in sapling heights

Changes in sapling heights were recorded from 1977-1998 (Figure 2). The overall trend was downward. Average height fell from 29.3cm to 10.6cm, maximum height from 91cm to 26cm, and no sapling grew above 122cm height.

Change in the height of the twelve saplings that attained 50cm height was examined (Figure 3). All were present in 1977, and nine were already 50cm tall. The three others grew to 50cm height by 1979, 1981 and 1983. Although seven survived for over a decade, mostly simply stagnated. In part this was because they were pruned back by livestock browsing. Destruction of these saplings increased from 1990. The last recorded sapling alive above 50cm height was in the spring 1991, and all had died off by the end of 1994.

Table 6: Average change in height for surviving saplings over each winter and summer period between 1977 and 1998.

Winter period	n	Average	Summer period	n	Average
25.11.77 - 2.5.78	49	-2.31	2.5.78 - 7.11.78	43	1.56
7.11.78 - 25.4.79	49	-5.80	25.4.79 - 29.10.79	43	-0.12
29.10.79 - 28.4.80	44	-2.57	28.4.80 - 30.10.80	41	1.15
30.10.80 - 30.4.81	38	-3.03	30.4.81 - 22.10.81	37	2.08
22.10.81 - 23.4.82	38	-1.55	23.4.82 - 27.10.82	36	-2.00
27.10.82 - 28.4.83	35	2.23	28.4.83 - 25.10.83	34	5.50
15.10.84 - 24.4.85	44	-1.80	24.4.85 - 15.10.85	35	0.63
15.10.85 - 22.5.86	43	-2.56	22.5.86 - 10.10.86	34	0.71
10.10.86 - 21.4.87	35	-1.77	21.4.87 - 26.10.87	28	1.36
26.10.87 - 4.5.88	28	-1.14	4.5.88 - 17.10.88	26	1.12
17.10.88 - 26.4.89	23	-1.74	26.4.89 - 10.10.89	21	-5.19
10.10.89 - 23.4.90	21	-1.62	23.4.90 - 18.10.90	15	6.07
18.10.90 - 10.5.91	19	-3.95	10.5.91 - 22.10.91	14	-1.86
22.10.91 - 11.5.92	15	-0.13	11.5.92 - 9.10.92	11	2.45
9.10.92 - 11.3.93	10	-3.10	11.3.93 - 25.10.93	7	-0.14
25.10.93 - 26.4.94	5	-6.20	26.4.94 - 12.10.94	4	2.25
12.10.94 - 11.4.95	5	-2.20	11.4.95 - 23.10.95	3	5.00
23.10.95 - 30.4.96	3	-2.00	30.4.96 - 18.10.96	3	3.00
18.10.96 - 2.5.97	28	-3.21	2.5.97 - 21.10.97	24	0.21
21.10.97 - 14.5.98	16	-0.25	14.5.98 - 7.10.98	13	1.00

Reduction in sapling height tended to occur most over winter periods: 58% of all recorded winter height changes and most average winter height changes were negative (Table 6). Total winter height change was negatively correlated to sapling density, average height, and total height at the start of each winter (Table 5), i.e. height loss was greater where initial density and biomass were high. Sapling heights tended to increase over summer periods, but the overall average was just 0.94cm. Although 54% of summer height changes were increments, 13% showed no change, and 33% showed a reduction in height.

Discussion

Changes in the sapling population

The sapling plot in Wistman's Wood was initially located in an open glade surrounded by trees, where a sapling bank had established in the face of stock grazing. During the 25 years of observations there was a large input of new oak saplings following mast years on average every 4 years. This is within the range cited for lowland situations where uniform heavy and moderate acorn crops occur typically every 6-7 and 3-4 years respectively (Jones 1959; Worrel & Nixon 1991).

Although germination continued unabated throughout the period of observation, many germinants died within a year and most survivors lasted only a few more. Progressively, mortality rates increased, sapling height decreased, and the average age of saplings and the number of established saplings (5 years old or more) both decreased. Only one sapling survived from the original population, and this was in poor condition in 1998. There was no recruitment to the stand, i.e. no saplings managed to grow above the reach of grazing animals, and the possibility of successful recruitment diminished steadily. In 1973 the population may have been close to successful regeneration, with at least one individual 1m high, but by 1998 the prospect of success was negligible.

Grazing

This decline in the prospects for successful regeneration can easily be ascribed to increased grazing. At the start of the study, cattle frequented the plot in both winter and summer, which resulted in considerable yarding and dunging. Although stock numbers were not recorded during the study, the changes in the amount of dung and bare soil in the plots indicated that cattle numbers increased during the 1980s, remained high until autumn of 1995, and that cattle frequently used the wood during the winter.

Stock directly grazed saplings and, most importantly, pruned back all of the tallest saplings. Short saplings may also have been grazed off by stock and killed: the three largest episodes of high sapling mortality, the overall downward trend in sapling numbers, and the simplification of the age-structure all occurred when grazing appeared to have been high. Also, the limited improvement in the sapling age-structure and the occurrence of holly and rowan saplings, two particularly palatable species, coincided with the reduction in grazing pressure. Certainly, young oak saplings have a lower likelihood of survival when they are grazed by ungulates (Van Hees *et al* 1996).

Grazing appeared to have occurred throughout the year. During the winter periods many saplings were reduced in height, and even during the summer growth period few saplings extended much in height and many actually declined. A positive correlation existed between summer sapling mortality and initial sapling density and total height, but winter mortality showed no relationships. This indicates that mortality was greatest when saplings were in leaf, i.e. when they were most apparent.

The cattle also caused disturbance to the ground vegetation. They knocked mats of moss off boulders, and thus were probably the cause of the slight decline in moss abundance during the 1980s and early 1990s. With increased grazing, common bent and bracken declined, wavy hair-grass increased slightly, and creeping soft-grass invaded. Creeping soft-grass readily invades disturbed ground (Grime *et al* 1990), such as that poached by cattle, and will increase in consistently grazed stands (Rodwell 1991). Although increased shading would have weakened bracken, changes in grazing are also implicated in its decline (Grime *et al* 1990; Rodwell 1991). Certainly, a file note in March 1993 stated that cattle had been physically damaging bracken by flattening it.

Shading

Another factor in the decline in the sapling population was increased shading. During the period of observation, the plot changed from an open glade into a small gap surrounded by heavy shade, with only the edge of one gap persisting throughout. This would have influenced the ground vegetation, and was probably instrumental in reducing the cover of bracken (Watt 1976; Rodwell 1991). We assume that the vigour of oak saplings would also have declined, increasing the effects of mildew, insect and stock defoliation, and thus reducing their chances of survival (Watt 1919; Jarvis 1964; Shaw 1974; Newbould 1983; Worrel & Nixon 1991; Van Hees *et al* 1996; Humphrey & Swaine 1997).

Regeneration in Wistmans Wood

Does Wistmans Wood need to regenerate? Put another way, should one expect recruitment to the stand in the absence of heavy grazing? Earlier this century when grazing appeared to have been low, substantial recruitment of oak took place on the margins of the old oak stands on clitter (Proctor *et al* 1980). This marginal regeneration continued until the mid-1970s, but was subsequently curtailed by increased livestock grazing (Mountford 1999). Within established closed stands and in gaps in the old stands there has been no oak regeneration recorded, and where the old stands are breaking up it is doubtful whether oak recruitment would occur even in the absence of sustained heavy grazing. Only rowan has successfully established in shaded conditions, and then only in inaccessible locations or when grazing was low (Mountford 1999).

Research and monitoring

The observations in this study represent a description of oak sapling demography under heavy browsing pressure in a gap that was steadily reduced by crown growth of marginal trees. We know of no comparable observations, and to that extent the study increases our knowledge of oak performance in Britain.

The plot itself is fairly central to the wood and is as representative as a single plot can be, but other types of ground (e.g. wholly shaded ground below oaks; marginal grassland and bracken areas) were not observed in the same detail. Site managers nevertheless made informal comparisons between the observed plot and the rest of the wood.

Since no successful recruitment to the stand took place, is has not been possible to construct a regeneration index for future use or use elsewhere. Had there been a period of recruitment, it would have been possible to look for an index, such as the average height of the five tallest saplings. The trend in this possible index suggests that an average height something above 70cm may indicate the threshold of recruitment.

Is it worth continuing the observations? Assuming that resources for recording will always be limited, this can only be fully answered against an appraisal of competing claims on recorders' time. Perhaps the best solution would be to maintain the present plot, but with autumn observations only, and to use the time saved to establish several similar plots scattered in the bracken-fringed area outside the wood, i.e. where recruitment is most likely to take place in an environment of reduced grazing (Proctor *et al* 1980; Mountford 1999). Within these it would be useful to; 1) map physical features within the plot; 2) record individual saplings as in the existing plot, but supplement this with information on the cause of shoot reduction, decline and mortality (e.g. grazing by livestock, debarking by voles, dieback, mildew, defoliation); 3) record changes in the ground cover as per the existing plot (major vegetation species, dung and bare ground), but supplement this with information on the direct causes of change (e.g. cattle trampling); and 4) record the stock types and numbers in summer and winter within the intake.

This type of study complements studies of stand structure recorded by means of permanent plots recorded at intervals of about a decade. Recruitment in these is formally recorded when new stems and individuals reach 1.3m height, i.e. once plants have got through the initial stages described here.

References

ARCHIBALD, J.F. 1966. First management plan for Wistman's Wood Forest Nature Reserve, Devon. Unpublished report, Nature Conservancy (held by English Nature at Yarner Wood Office).

BENNET, K.D. 1989. A provisional map of forest types of the British Isles 5000 years ago. *Journal of Quaternary Science*, **4**, 141-144.

BRUNSDEN, D. 1964. The origin of the decomposed granite. *In*: Simmons, I.G., ed. *Dartmoor Essays*. 97-116. Exeter: Simmons.

CHRISTY, R.M. & WORTH, R.H. 1992. The ancient dwarfed oak woods of Dartmoor. *Transactions of the Devonshire Association for the Advancement of Science, Literature, and Art,* **54**, 291-342.

ECOSCOPE APPLIED ECOLOGISTS. 1999. Monitoring requirements and methods for woodland, scrub, lowland wood pastures, parkland, trees and woodland stands. Unpublished draft document, Ecoscope Applied Ecologists.

GREENSLADE, P.J.M. 1968. A note on Wistman's Wood, Dartmoor. *Proceedings of the Botanical Society of the British Isles,* **7**, 159-163.

GRIME, J.P., HODGSON, J.G. & HUNT, R. 1990. *The Abridged Comparative Plant Ecology*. London: Chapman and Hall.

HALL, J.E., KIRBY, K.J. & MORECROFT, M. 1999. *Minimum intervention woodlands and their use for ecological research in Great Britain.* Peterborough: Joint Nature Conservation Committee (JNCC Report 295).

HUMPHREY, J.W. & SWAINE, M.D. 1997. Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods. II. Insect defoliation of trees and saplings. *Journal of Applied Ecology,* **34**, 585-593.

JARVIS, P.G. 1964. The adaptability to light intensity of saplings of *Quercus petraea* (Matt.) Liebl. *Journal of Ecology,* **52**, 545-571.

JONES, E.W. 1959. Biological Flora of the British Isles: *Quercus* L. *Journal of Ecology,* **47**, 169-222.

MOUNTFORD, E.P. 1999. Long-term change in a near-natural upland oakwood: Wistman's Wood National Nature Reserve. Unpublished report, Ecoscope Applied Ecologists.

NEWBOULD, A.J. 1983. Some aspects of the regeneration of oak and beech. Unpublished Ph.D. Thesis. London, University College.

PETERKEN, G.F. 1981. *Woodland Conservation and Management.* London: Chapman and Hall.

PETERKEN, G.F. & BACKMEROFF, C.E. 1989. *Long-term monitoring in unmanaged woodland nature reserves.* Peterborough: Nature Conservancy Council. (Research and Survey in Nature Conservation, No. 9).

PROCTOR, M.C.F., SPOONER, G.M. & SPOONER, M. 1980. Changes in Wistman's Wood, Devon: photographic and other evidence. *Transactions of the Devonshire Association for Science, Literature and Art,* **112**, 43-79.

RODWELL, J.S. 1991. *British Plant Communities. Volume 1: Woodlands and Scrub.* Cambridge: Cambridge University Press.

ROBERTS, D. & MARREN, P. 1971. Report on a survey of Wistman's Wood, Devon. Unpublished report, Exeter University (held by English Nature at Yarner Wood Office).

SHAW, M.W. 1974. The reproductive characteristics of oak. In: MORRIS, M.G. & PERRING, F.H., eds. *The British Oak: its History and Natural History* 162-181. Faringdon: Classey.

SIMMONS, I.G. 1964. Pollen diagrams from Dartmoor. *New Phytologist,* **63**, 196-180.

SIMMONS, I.G. 1965. Dartmoor oak copses. *Field Studies,* **2**, 225-235.

TANSLEY, A.G. 1939. *The British Isles and their Vegetation.* Cambridge: Cambridge University Press.

VAN HEES, A.F.M., KUITERS, A.T. & SLIM, P.A. 1996. Growth and development of sliver birch, pedunculate oak and beech as affected by deer browsing. *Forest Ecology and Management,* **88**, 55-63.

WATT, A.S. 1919. On the causes of failure of natural regeneration in British oakwoods. *Journal of Ecology,* **7**, 173-203.

WORREL, R. & NIXON, C.J. 1991. *Factors affecting the national regeneration of oaks in upland Britain - A literature review.* Occasional Paper 31. Edinburgh: Forestry Commission.

WATT, A.S. 1976. The ecological status of bracken. *Botanical Journal of the Linnean Society,* **73**, 217-240.